## VI.—*General Observations on Fission and Gemmation in the Animal Kingdom.* By Dr. Franz von Wagner, Assistant in the Zoological Institute of the University of Strassburg *.

### I.

The asexual reproduction of the Microstomids, as described in the foregoing pages, has been hitherto theoretically claimed by the different investigators sometimes as gemmation, sometimes as fission.

If we disregard Œrstedt †, who probably merely observed the folding of the intestine which is connected with the formation of septa, Oscar Schmidt was the earliest investigator of the multiplication of the Microstomids.

His diagnosis of the family "Microstomeæ" states ‡: "Reproduction by transverse fission." Moreover, in his description of the reproduction Schmidt characterizes it exclusively as fission. But even in the same year (1848) this investigator writes as follows §:—"I have designated the well-known multiplication of the Naids and Microstomids simply as transverse fission, although a glance at my figures will show that with this transverse fission is combined longitudinal growth of the portions which are to be constricted off. That, however, a part of the parent of those Turbellarians really passes into the new animal appears to me to be indisputable." But immediately afterwards (*loc. cit.* p. 37), when discussing the reproduction of *Filograna*, the same author states:—"If anywhere at all, it is here, at least in the case of the *Filograna* examined by me, that we see with especial clearness that the actual transverse fission is the least important stage in the development of the new animal, and that, on the contrary, the latter grows as a true bud or sprout upon

* Translated from the 'Zoologische Jahrbücher—Abtheilung für Anatomie und Ontogenie der Thiere,' 4 Bd. Heft iii. Dec. 1890, pp. 386–417: being the latter portion of a paper by Dr. Wagner, entitled "Zur Kenntniss der ungeschlechtlichen Fortpflanzung von *Microstoma*, nebst allgemeinen Bemerkungen über Theilung und Knospung im Thierreich," *ibid.* pp. 349–423 (with four plates).

† A. S. Œrstedt, 'Entwurf einer systematischen Eintheilung und speciellen Beschreibung der Plattwürmer,' Copenhagen, 1844, p. 73.

‡ O. Schmidt, 'Die rhabdocœlen Strudelwürmer des süssen Wassers,' Jena, 1848, p. 22.

§ O. Schmidt, 'Neue Beiträge zur Naturgeschichte der Würmer,' Jena, 1848, p. 36.

the parent, and has its alimentary canal in common with it, as in the case of the old and young *Hydra* before separation has taken place.

In the last (1882) edition of his 'Vergleichende Anatomie' * Schmidt again designates the asexual reproduction of *Microstoma* (as also that of the Naidæ) simply as fission.

In 1849 M. Schultze declared very emphatically that the multiplication of the Microstomids, like that of *Nais*, "depends not upon a mere formation of buds, but upon a constriction of a single animal into several, progressing according to perfectly definite laws" †. Like Schmidt, Schultze also herein attached most importance to the fact that "in this there takes place an actual separation of a portion previously belonging to the parent to form a new individual" (*loc. cit.* p. 294).

Von Graff, in his 'Neuen Mittheilungen über Turbellarien' (1875), in which we find the first exact description of the asexual reproduction of *Microstoma*, regards the process as fission, without making any further observations on the point‡.

Von Graff's results were supplemented, in some cases rectified, by the important investigations of P. Hallez, in particular by the discovery that it is always the posterior third of the body of the multiplying animal which represents the rudiment of the new zooid §.

Von Graff was subsequently able to confirm this discovery, but it induced him, in his great Monograph of 1882, to declare the multiplication of Microstomids to be a case of gemmation. The following sentences || convey the essence of his view:—"The . . . . asexual reproduction of *Microstoma lineare* is undoubtedly to be regarded as gemmation, and indeed as a terminal formation of buds, in which the posterior end of the parent 'grows and separates itself off as a young individual from the old,'" so that therefore "'the younger terminal bud'" is "'subordinate to the older parent individual.'"

"It was not until Hallez discovered the fact that it is always only the posterior third or fourth of the parent, therefore that portion which we may as it were regard as the

* O. Schmidt, 'Handbuch der vergleichenden Anatomie,' 8 Aufl., Jena, 1882, p. 107.

† M. Schultze, "Ueber die Fortpflanzung durch Theilung bei *Nais proboscidea*," Arch. f. Naturgesch. 15 Jahrg. Bd. i. p. 294.

‡ L. Graff, "Neue Mittheilungen über Turbellarien," Zeitschr. f. wiss. Zool. Bd. 25, pp. 409 *et sqq.*

§ P. Hallez, 'Contributions à l'histoire naturelle des Turbellariés,' Lille, 1879, pp. 153 *et sqq.*

|| L. v. Graff, 'Monographie der Turbellarien.—I. Rhabdocœlida,' Leipzig, 1882, p. 174.

increase due to growth over and above the limits of the individual, which separates off from it, that the character of this reproduction as a process of terminal gemmation was made plain. That it is a case of terminal gemmation with which we have to deal is emphasized even more definitely by the fact that the parent, however many buds it may produce, never decreases in size. On the contrary, the size is always equal to that of solitary individuals, which I have observed before the appearance of any indication of budding, or at the very commencement of it. . . ."

This view has hitherto met with much approbation.

Yet opposition, though indeed more of an occasional kind, has also been meted out to von Graff's gemmation theory.

Thus Count Zeppelin, in his paper on *Ctenodrilus monostylos* * (1883), observes :—" The erroneous view previously held, that reproduction by fission in the Worms depends upon mere gemmation, has been overthrown by O. Schmidt for the Microstomids, which belong to the Rhabdocœle Turbellaria, since in these animals there takes place an actual separation of a portion previously belonging to the parent. The incorrectness of this theory is similarly proved by the processes of fission which are found in *Nais*, *Chætogaster*, *Ctenodrilus*, &c., in which the hindmost section of the body passes unchanged into the new creature. In these animals a genuine fission occurs, while in *Autolytus*, *Filograna implexa*, *F. Schleideni*, *Myrianida*, and others the young individuals sprout forth as buds upon the parent form without including in themselves integral constituent parts of the latter. In this case therefore a true gemmation takes place."

Count Zeppelin therefore agrees with O. Schmidt and M. Schultze in regarding the direct transition of a portion of the parent into the daughter individual as the crucial test of fission.

It is essentially from the same point of view that Goette, *à propos* of his investigations into the ontogeny of *Aurelia aurita*, pronounces the reproduction of the animals which we are discussing to be a process of " successive fissions " †.

Claus, too, in the different editions of his well-known manual, always treats the asexual reproduction of *Microstoma* substantially as (transverse) fission, although it is true no great weight can be attached to this, since this author by no

* Graf Zeppelin, " Ueber den Bau und die Theilungsvorgänge des *Ctenodrilus monostylos*, nov. spec.," Zeitschr. f. wiss. Zool. Bd. 39, p. 645.

† A. Goette, 'Entwicklungsgeschichte der *Aurelia aurita* und *Cotylorhiza tuberculata*,' Leipzig, 1887, p. 48.

means makes a strict distinction between fission and gemmation (*cf.* note *a*, below).

The above historical sketch, all incomplete though it is, renders sufficient evidence of the uncertainty which blocks the way of an absolute criticism of the reproduction of *Microstoma*; so that in spite of the material progress which has been effected in our knowledge of the process since the investigations of Schmidt, the theoretical interpretation of the subject (like that of many similar processes in other animals, especially worms) appears to have been in no way advanced.

This surprising state of things is due not so much to the peculiar phenomena presented by the asexual reproduction of *Microstoma*, as to the general fact that uncertainty has arisen as to what is to be regarded as fission and what as gemmation. This uncertainty, it is true, appeared latterly to have been abolished by the view, which met with constantly widening acceptance, that fission and gemmation are processes which are most intimately related to one another. As a result of this the question whether in a particular case this or that interpretation was correct naturally lost its importance (note *a*).

Nevertheless the view which maintains that fission and gemmation are fundamentally only two different representations of one and the same form of reproduction does little more than clothe the old uncertainty in a new garb; for if we would discover relations of whatsoever kind between fission and gemmation we must first have come to an understanding as to the essential characteristics of the two reproductive methods. Yet every one who is acquainted with the subject is aware how little this condition is fulfilled at the present time. The manuals are lacking in precise statements*; in particular cases we help ourselves by distinguishing, *e. g.* in the Syllidæ and their allies, a "fissiparous" from a "gemmiparous" reproduction, or by paraphrasing so-called

*a*. Thus the question whether the strobilation of the Medusæ is to be regarded as simple transverse fission or as terminal gemmation appears to Claus "to be in itself a case of splitting hairs."—C. Claus, 'Untersuchungen über die Organisation und Entwicklung der Medusen,' Leipzig, 1883, p. 17.

* The present paper was practically completed when I came across Heft 2 of Hatschek's 'Zoologie.' The observations of this author upon fission and gemmation contain a wealth of appropriate standpoints for the consideration of the question, and I hasten to refer the reader to them, at any rate for the sake of comparison, since a detailed discussion of his remarks would here lead us much too far afield, considering the difference in our fundamental ideas of the processes (*cf.* Hatschek, 'Lehrbuch der Zoologie,' Heft 2, Jena, 1889, pp. 216 *et sqq.*).

"terminal gemmation" as "growth in the longitudinal axis with subsequent transverse fission" *, &c.

To proceed to generalizations before we have acquired complete clearness as to fundamental notions is always a critical undertaking. I therefore hold it to be absolutely indispensable, though other investigators may perhaps at once consider it superfluous, to find out what we are to term fission and what is to be designated as gemmation.

Since I was thus of necessity led, from the interpretation of the reproduction of *Microstoma* in particular, to a general investigation of the doctrine of fission and gemmation in the whole Animal Kingdom, a simple consideration indicated the path which I had to adopt for the latter. It was self-evident that it was not a question of somehow or other distinguishing fission and gemmation from one another, but of demonstrating the natural characteristics of the two forms of reproduction, or at least of one of them. "Natural" characteristics are, however, those which, in the notional meaning of the term, which is also otherwise united therewith, admit of being enumerated without compulsion.

The word "gemmation" denotes exclusively biological processes, to which there is nothing corresponding outside organic nature. Nevertheless, owing to the multifarious and consequently ambiguous application of this expression, it is absolutely impossible to state what gemmation signifies within the limits of the Animal Kingdom. In one case tentacles "bud" upon a polyp, in another proglottids from a scolex, in a third segments at the growing hinder end of an Annelid, or, again, whole individuals or parts thereof "bud" from and upon a parent, and in the ontogeny of Vertebrates we even meet with a "caudal bud." The only feature in common which all these different processes can well have is that *something, somewhere and somehow, grows upon an animal.*

I therefore reverted to "fission," a word with which everyone connects a distinct idea, which is first acquired outside the vital processes. This gives us an objective foundation for further developments.

The following statements therefore proceed from the starting-point of fission. I have put them as shortly as possible, because I did not wish to prolong the present paper to an unseemly length.

Whether the attempt which I have made to establish a

* C. Claus, 'Untersuchungen über die Organisation und Entwicklung der Medusen,' Leipzig, 1883, p. 17.

natural conception in the doctrine of asexual reproduction by gemmation and fission in the place of the confusion and arbitrary interpretations which have hitherto existed will meet with any approval among my fellow scientists the future will decide; it would be enough for me if a stimulus should thereby be given which shall cause better insight and more comprehensive information than I myself possess to win a knowledge of the truth.

## II.

According to the meaning of the word, "fission" signifies the simple separation of one (or more) portions from an integral whole, therefore the division of an originally united whole into two or more parts. If we cut a block of stone into three portions we effect a fission: the process of separation itself is the fission. Herein it makes no difference whether the sections which now exist are of the same size or not and whether they were actually produced simultaneously or one after another. If for the block of stone I substitute a crystal which is *in statû nascendi*, and therefore continually increasing in size or growing, and cut it into three pieces, this is equally a fission. The concurrent increase in size, or growth, does not affect the process; it is a natural property of the crystal and is a normal phenomenon.

The idea conveyed by the term fission as applied to the inorganic body (and as it is also applied in daily life) is thus exhausted with the actual process of division, and is seen to be independent of:—

(1) The size of the fission products;

(2) The time of their origin; and

(3) The presence or absence of a normal increase in size (growth).

In order to be able to transfer to organisms the conception of fission which we have gained, an appeal might be made to the fact that people have been induced to designate as fission certain forms of reproduction in animals, precisely because they corresponded to the usual interpretation of this expression. But if, among the asexual modes of animal reproduction, we should succeed in finding one (or more) which would admit of being classed as fission without straining the limits of the conception as enunciated above, not only would the intended transference be justified thereby, but

also a starting-point would be gained in the Animal Kingdom itself from which we could criticize other methods of propagation; for we should still have to separate the material in them from the immaterial and to distinguish the primary from the newly acquired.

Among the Metazoa such an attempt is useless, since even the least complicated form of asexual reproduction which occurs in this group, the simple breaking up of *Lumbriculus*, exhibits phenomena (regeneration) in connexion with the multiplication which at once exclude the possibility of identifying the process with the fission of inorganic bodies.

With regard to the Protozoa the case is different: here we actually find the desired starting-point. The fission of an Amœba coincides exactly as regards the outward phenomenon and its consequences with that of the block of stone or crystal: the process itself and the relations to size, time, and growth are the same in each case. The only difference is objective and does not affect our argument; it lies in the fact that the effect, which in the case of the block of stone is produced by the hand of man from the outside, results in the Amœba from internal causes having their origin in the organism itself.

Since, therefore, both instances of fission are similar processes, the fission of the Amœba also consists in the actual process of division. I will term this simplest form of fission, which we may also hold to be the earliest, "*architomy*" (i. e. "*primary form of fission*").

Nevertheless among the modes of reproduction found in the Protozoa there are also some which appear to diverge considerably from the architomic type, and yet from the earliest times they have been declared without contradiction to be instances of fission. We will briefly consider two of these cases.

The reproduction of certain Infusoria takes place in such a way that an envelope or cyst is differentiated within which the processes of fission are carried out. The latter, considered by themselves, belong to the architomic class; but in connexion with them we get the further phenomenon of the above-mentioned formation of the envelope. Clearly the true question which is here raised is this: Is the formation of a cyst the expression of a new principle, when contrasted with which the fission becomes of secondary importance, or may we interpret it as an adaptation of one of those vital phenomena otherwise known to us in these animals, which is here brought into harmony with and subordinated to the process of fission? There never was any doubt about rejecting the

former and accepting the latter of these hypotheses. We justly regard the secretion of a cyst as a protective formation secondarily acquired and owing its origin to the existence of fission.

The majority of Infusoria, such as *Stentor* for instance, preserve their species by means of a form of fission in which the formation of a new peristome and pharynx is to be observed in one of the two animals in process of development. Phenomena of this nature, which we shall meet with in the fission of higher animals of all kinds, have long been included under the term "*regeneration*." The question which we put in the case of cystic fission leads to a similar answer when applied to the mode of reproduction found in *Stentor*. The regeneration of the organs which we have mentioned does not imply something fundamentally new, but is a consequence which necessarily results from the organization of the dividing animal, the effect of which is to enable the posterior zooid to maintain an independent existence. It is easy to see from the context that in the case of the anterior fission-product, which is from the first in possession of the original structures and therefore of the conditions of an independent life, no, or, to be more exact, scarcely any, regeneration is necessary.

The examples which have been adduced show that certain forms of fission in the Protozoa include accessory processes, among which the phenomena of regeneration at least are seen to be *necessary*, and in many cases of fission must attain the importance of a *conditio sine quâ non*. In consequence of this, however, that which in the case of the Amœba is effected by the fission, the actual process of division—originally a form of reproduction in itself—becomes in the case of *Stentor* a stage in the fission of this Infusorian, which is also characterized by regeneration. The latter mode of reproduction, therefore, when contrasted with that of Amœba, signifies a higher and more advanced form of fission, and may be designated as "*paratomy*" (i. e. "*secondary form of fission*"), as opposed to architomy. The process of division, which is the essence of architomy, appears as a stage in paratomy as "*dissection*" or "*separation*."

I now proceed to the consideration of another mode of reproduction among the Protozoa, namely gemmation. The multiplication of *Podophrya* may serve as an example.

We are here confronted with a phenomenon which is not to be understood from the ensemble of the points of view which we have adopted for the consideration of fission, and is therefore virtually new: this is *a special kind of growth*. While in the case of Amœba and *Stentor* the increase in size,

which happens to take place concurrently with fission and which I previously neglected for the sake of simplicity, offers no peculiarity, the growth which leads to the formation of a bud in *Podophrya* differs from the very first from the normal increase in size in this Acinetarian. The growth of the Acinetarian buds is limited in extent to isolated spots on the surface of the body of the budding parent-form: *it is not the growth of the* Podophrya, *but a growth upon it, by the side of which the former continues, or may continue, to exist.*

It is advisable, for the sake of simplifying matters, to sharply distinguish this bud-growth under the title "*differential*" from the normal or "*individual*" growth.

*Differential* growth appears to a certain extent as transcending the organization and personality of the budding parent-form, and therefore implies no increase of size for the latter; precisely on this account it necessarily leads to the production of a new individual: *in its simplest form* it in no way affects the organization and individuality of the budding animal, as, for instance, is manifest in the case of *Hydra*. As opposed to this, *individual* growth entails an actual increase in the size of the animal which is sooner or later to divide; but this coincides with the form of growth which belongs to this organism, since it actually represents nothing more than the natural increase in size (*normal* growth) of the creature in question, whether simultaneously or subsequently asexual reproduction sets in or not.

In this connexion also I would at the same time emphatically point out that it is not the direction of growth which constitutes the entire difference, as it might appear on a superficial consideration of the circumstances of asexual reproduction. As a matter of fact the buds of Acinetarians also make this clear, since their growth essentially takes place in the normal direction of that of the parent, and yet in no way represents a simple increase in the size of the latter.

The multiplication of Acinetarians thus proves itself to be a form of reproduction which differs from fission, and is *in its essence solely and sufficiently determined by the appearance of a special form of growth, which we have termed differential.* This peculiarity is certainly important enough to warrant our designating such processes by a special name: I merely follow old custom in embracing them under the comprehensive term "*gemmation.*"

That which reminds us of fission in these cases is simply the process—the severance—by which the bud becomes a free independent being, an act within this asexual mode of reproduction, which is far more often omitted than performed,

whereby its subordinate importance appears sufficiently established (formation of colonies in Metazoa).

Although I have hitherto spoken of the Protozoa, it was far from my intention in so doing to pronounce judgment upon the forms of reproduction in these animals, which so greatly overlap one another, especially since scarcely anything can be added to the classic statements contained in Bütschli's great work; it is, on the contrary, more in accordance with the plan of these explanations briefly to consider, by the aid of a few characteristic examples, reproductive conditions of the simplest kind, which are not without value for the comprehension of the asexual propagation of the Metazoa. The following arguments refer solely to the Metazoa, and claim validity for these alone. I therefore think it desirable, since I consider a sharp separation of fission from gemmation to be possible for the higher animals, and shall exert myself to accomplish the same, to declare emphatically at this point that as regards the Protozoa I side unreservedly with those who hold that fission and gemmation merge into one another in these simplest forms of animals, and who therefore decline to draw a strict distinction between them within this branch of the Animal Kingdom. In this connexion it will be readily understood that in proceeding with the views which we have just acquired to the domain of the Metazoa I do not wish to convey that the fission and gemmation of the higher animals are to be referred phylogenetically to the similarly named processes in the Protozoa.

At the gate of the Metazoon kingdom stands the so-called *process of segmentation* (fission of the ovum). Although this has no direct relation to asexual reproduction, it will nevertheless be useful for our purpose to bestow a brief consideration upon it.

The segmentation of the ovum has invariably and without contradiction been regarded as fission, even where "so typical a picture of gemmation is exhibited as can only be presented by an Acinetarian among the Protozoa"*. It is clear that "if from certain large cells there actually grow out small portions, which are gradually constricted off"*, such a process, provided it really takes place, coincides far more with the idea of gemmation than with that of fission. In spite of this we speak even in such cases, and rightly, of a fission of the ovum, since the growth which thereby appears is the normal growth for the ovum in question, and must indeed be

* J. v. Kennel, 'Ueber Theilung und Knospung der Thiere,' Dorpat, 1888, p. 11.

so, since it does not possess any other kind. The essence of gemmation, however, lies precisely in this, that the growth peculiar to it is added as a new process to the normal phenomenon.

Moreover, no matter what views we may hold as to the evolution of the Metazoa from the Protozoa, we are bound to recognize in the fission of the ovum a recapitulation of the typical fission of the Protozoa, which thereby passes from a form of reproduction into a mode of multiplication for tissues.

The segmentation of the ovum thus teaches us that the expression fission is also applied in the same sense outside the phenomena of reproduction.

For the investigation of reproduction by fission and gemmation in the Metazoa the course which we adopted in the case of the Protozoa is impracticable for obvious reasons. I shall therefore in the first place attempt to gain standpoints for a general consideration of the question, and in so doing briefly refer to concrete examples only where it is necessary.

The cases of asexual reproduction by fission and gemmation which have so far been discovered in the domain of the higher animals admit quite well of being connected with the similar conditions which exist among the Protozoa.

Firstly with regard to fission: the modifications of the original form of fission, architomy, which arise among the lower animals, undergo extensive development in the Metazoa. The higher stage of organization existing in these animals entails the impossibility of architomy in their case; the processes of regeneration which are connected with almost all cases of fission among the Metazoa cause those modes of reproduction to appear rather as instances of paratomy when contrasted with what happens in the case of *Stentor*.

In the fission of the higher animals *three* stages may be distinguished, which both in themselves, as also in their relation to one another within a case of paratomy, require more detailed discussion. They are, firstly *regeneration*, secondly *separation* (*dissection*), and thirdly *growth*.

That the *regeneration* which in the case of *Stentor* combines with the separation to form an harmonious whole must in the Metazoa advance into the foreground in proportion as the organization of the proliferating animals becomes more complicated, is so natural a circumstance that we should be surprised if it were otherwise.

Now as the measure of the work to be performed by regeneration in organs and parts of organs, which must necessarily be reconstructed, becomes constantly greater, it is self-evident that the process of separation will sink in the

same degree in the outward manifestation of the fission, until at last it assumes the position of a more secondary final act.

There is a natural inclination on the part of the observer of this class of fission to regard the extensive reconstructions as the essence of the process, while considering as of trifling moment the uninteresting separation.

It is, however, other things being equal, not so much the extent as the nature of the regenerations which causes many cases of fission to be interpreted as gemmation. Thus gemmation is especially discovered in all kinds of worms, whereas, so far as my own conviction goes, in these animals, with perhaps the sole exception of the remarkable reproduction of *Syllis ramosa*, with which M'Intosh has made us acquainted*, fission alone occurs.

For, on observing the course of the regenerations, manifold features are seen, which are found in the formation of a number of organs in the ontogeny of many animals, and which we are wont to term in ordinary phraseology "sprouts" or "buds." Of the extent to which this outward similarity of what are at the bottom very different processes is taken as internal homogeneity, owing to the consonance of their designations, the Naids are a classic example. The gemmation which is alleged to exist among these worms reduces itself to the appearance of so-called "zones of gemmation" in their asexual reproduction. Herein it must remain undecided whether this multiplication is to be regarded as "gemmation," because "zones of gemmation" are formed, or whether, on the contrary, these latter receive their designation because the whole process is to be taken as an instance of gemmation. The "zones of gemmation" of the Naids are, however, nothing more than *zones of regeneration*, within which proceeds the development of organs and parts of organs, which is necessarily combined with paratomy. That the latter is an actual new formation is in accordance with the nature of the case; it is related to the fission of the Naid in precisely the same way as is the formation of peristome and pharynx to the reproduction of *Stentor*. If, therefore, we speak of such processes as fission depending upon "gemmation" or "processes of gemmation" †, we do not use the expression "gemmation" in the sense of the mode of

* "Report of the Scientific Results of the Voyage of H.M.S. 'Challenger,' Zoology," vol. xii. pp. 198 *et sqq.*

† Thus, according to Vogt and Yung, the asexual reproduction of *Microstoma* consists "of repeated transverse fissions, and proceeds from axial budding at the posterior end" (C. Vogt and E. Yung, 'Lehrbuch der praktischen vergl. Anatomie,' i. p. 284, Braunschweig, 1888).

reproduction defined thereby, and consequently are not entitled to consider the two ideas as equivalent to one another. It would be more correct and would help to avoid erroneous conceptions were we to abandon the word "gemmation" altogether in such a sense, and simply designate the new formations as what they actually are, namely regenerations.

That the so-called zones of gemmation really deserve to be criticized in this way is most clearly shown by the cases in which such localized zones do not appear at all for the new formations which are necessary. This is seen in *Microstoma*, for example; quite peculiarly characteristic, however, is the different behaviour of the two species of *Ctenodrilus*, therefore of two Annelids which are most closely allied; in the case of one of these, *Ctenodrilus pardalis*, fission is ushered in by the appearance of the rudiment of a zone of regeneration *, while in the reproduction of the other such a process is absent, and the regenerations only proceed after the zooids have attained their independence†. *All these processes of new formation are the same in principle*, no matter whether they are accompanied or not by the development of special zones of regeneration.

The fission of *Haplosyllis spongicola*, however, which has been closely investigated by Albert, proves that the regenerations, and therefore also the special kind of them, can in themselves in no way determine the character of a case of asexual reproduction; for in the Syllid in question the "swimming buds," as they are called, which are detached and contain the sexual products, do not reproduce a special cephalic somite at all, but rather give rise to quite differently constituted new formations throughout their entire organization, so that the form and structure of these swimming zooids appear to diverge very considerably from that of the primary form ‡. In this connexion mention must moreover be made of *Clistomastus*, a Capitellid in which, as Eisig has informed us, the abdomen is constricted off filled with the ripe sexual products, although in these genital zooids neither new formations, as in *Haplosyllis*, nor regenerative processes appear, so that they represent extremely incomplete persons—so to speak

* J. Kennel, "Ueber *Ctenodrilus pardalis*, Clap.," Arbeiten a. d. zool.-zoot. Inst. in Würzburg, Bd. 5, pp. 395 *et sqq.*

† Graf Leppelin, "Ueber den Bau und die Theilungsvorgänge des *Ctenodrilus monostylos*, n. sp.," Zeitschrift f. wiss. Zool. Bd. 39, pp. 635 *et sqq.*

‡ F. Albert, "Ueber die Fortpflanzung von *Haplosyllis spongicola*, Gr.," Mitth. a. d. zool. Stat. zu Neapel, Bd. 7, pp. 10 *et sqq.*

mere genital tubes *. Similar conditions are also presented by the fission of the *Scyphostoma* (*Strobila* formation), in which the fission-products which successively arise are transformed from the original tentacle-bearing form into the lobed stage of the *Ephyra*.

The process of *separation*, as has already been stated, when contrasted with the more or less comprehensive regenerations, recedes in the same ratio into the background, especially where the paratomy is still further complicated by vigorous growth. As a rule separation constitutes the conclusion of fission, so that the development of the zooids which are set free is essentially complete. Occasionally, however, it ushers it in, as is partially the case in *Ctenodrilus monostylos*, but is especially seen in *Lumbriculus*. Von Kennel † has laid stress upon this condition, as he is moreover inclined to regard the fission of *Lumbriculus* not as a mode of reproduction, but as a simple augmentation. Nevertheless the observations which have been published by Bülow ‡ tend in one way rather to confirm the former view, though beyond this no special importance can be attached to the occurrence of so-called raw surfaces ("Wundflächen"), since these appear, although in a limited degree, in many cases of fission, and in fact are usually quite unavoidable. In *Microstoma* itself, for example, it is easy to convince ourselves that not infrequently quite a considerable raw place is to be seen, so that a destruction of tissues takes place at the spot.

With regard to *growth* it is to be remembered that it may accompany fission in so far as the growth is a property of the individual. The only question to be decided therefore is whether in a particular case the growth is individual or differential. Such a distinction is *at all times practicable* as soon as we grasp the fact that the bud, as such, proceeds from differential growth. I make this observation in opposition to the objection, improbable though it be, that the regenerations which have been discussed above arise in the same way.

The essential feature of gemmation-growth lies in its peculiarity of producing new individuals by being added to the normal growth; that it is also a growth which is confined to definite spots on the surface of the body of the parent form,

* H. Eisig, 'Monographie der Capitelliden des Golfes von Neapel &c.,' Berlin, 1887, pp. 794 *et sqq.*

† J. v. Kennel, 'Ueber Theilung und Knospung der Thiere,' Dorpat, 1888.

‡ C. Bülow, "Ueber Theilungs- und Regenerationsvorgänge bei Würmern," Archiv für Naturgesch. 49 Jahrg., Bd. 1, p. 28.

and is therefore local, is undeniable; *but it is not every instance of local growth that signifies gemmation.* It is necessary to exclude, firstly those regenerations which are localized upon zones of growth, and secondly the large number of processes of growth which, whether it be in consequence of simple elongation, or whether it be due to actual increase in bulk, are hereby restricted to an axis of the body (longitudinal axis). This course involves nothing that is arbitrary, but is rather a consequence of a logical necessity, since that increase in size represents the normal form of growth of the Metazoa in question and *takes place even in those cases where no asexual reproduction is combined with it.*

As regards the mutual relations of regenerations, separation, and growth in the course of a case of paratomy, I have already mentioned the variation which occurs in the time of the appearance of separation. With reference to this we might distinguish cases of paratomy with precocious regenerations from those in which they are of subsequent occurrence, were it not for the existence of the difficulty which is due to the fact that in many cases separation sets in when the first stages of the new formations have already commenced.

*The relation in time between the regenerations and growth* is here of special interest for us. In this respect the fission of the Naids is perhaps the most instructive and may serve as an example.

In the first place the growth of the Naid in process of fission appears everywhere as segmental and restricted to the longitudinal axis of the body of the animal, as is typical for the segmented worms; it is therefore an individual growth. But the extent of the increase in size, which is for the time being attained by the fission-products which are in process of formation, varies greatly, owing to the fact that the regenerations, that is the zones of regeneration, already appear before the growth of the zooids which are originated thereby has developed a trunk-section of any size (reproduction from the anal somite); or, in other words, that the point of time at which the rudiments of the zones of regeneration are developed appears to be transferred to constantly earlier stages in the size and therefore in the development of the future zooids. In consequence of such accelerations it is easy to form the impression that the fission-product grows out as a bud from the parent form. In connexion with forms of paratomy in the Naids which run a more regular course, however, these alterations in the order of time will become of so much

the less importance, since *the various processes themselves are the same in all cases.*

This conception of the reproduction of the Naids applies in corresponding fashion to the asexual reproduction by fission not only of the Annelids, but of the Worms in general, for there is no room for doubt that those modes of propagation are essentially of the same kind.

Now if an animal begins to divide and the regenerative processes in the zooids thus produced are quickly completed, and if, moreover, fission again sets in in the zooids themselves before they have attained their independence by means of the separation which is the concluding stage of the primary fission, the result naturally is a formation of temporary colonies, or, to speak more precisely, chains, since we are dealing with the transverse fission of animals which grow in their longitudinal axis. *The precocious commencement and retarded conclusion of fission, concurrently with rapid growth of the dividing animals*, are the circumstances which are chiefly responsible for the complicated and often very peculiar manifestations which are exhibited in the course of the asexual reproduction of many Metazoa. It is true that *secondary* causes are often added to these, since reproduction by fission may combine with transformations of the fission-products (strobilation of the Medusæ) or become more or less subservient to favourable sexual reproductive conditions; *this may result in the omission of regenerative processes and the occurrence of effective new formations* which did not belong to the original animal, but are of great service for the special purposes of the fission-products. An example of this is presented by, among others, the swimming zooids of the already mentioned *Haplosyllis*, which, in order to ensure the widest possible distribution of the sexual products, have equipped themselves with an exquisite locomotor apparatus *.

With regard to *gemmation* a few words only are necessary, for its character lies exclusively in the peculiarity of differential growth, so that all instances of gemmation, no matter whether we have to deal with a Polype, a Bryozoon, or a Salp, agree in this, though diverging widely in the details of the process. It is in consequence of this simplicity in the nature of gemmation as opposed to fission, which in many respects is subject to manifold changes, that the very different phases of development in which gemmation confronts us nevertheless invariably exhibit the same characteristic of special growth.

* F. Albert, "Ueber die Fortpflanzung von *Haplosyllis spongicola*, Gr.," Mitth. a. d. zool. Stat. zu Neapel, Bd. 7, pp. 12 *et sqq.*

It follows as a matter of course from what has been stated that gemmation by no means excludes the direct transition of a portion of the parent into the rudiment of the bud. As a matter of fact this actually occurs in the reproduction of certain Stony Corals, for an account of which we are indebted to the beautiful investigations of von Koch *.

In the foregoing statements as to fission and gemmation I have, in order to avoid too great complication of the progress of the discussion, disregarded a circumstance which nevertheless requires to be shortly considered in order to complete the views which we have gained, *i. e.* the question of *individuality.*

Hæckel was probably the first to establish the fact that, contrary to what happens in the case of fission, which disposes of the original parent-form, the individuality of the bud-producing animal is preserved unaltered. The general truth of this proposition is beyond question; in the case of gemmation it is proved by experience, in that of fission it is *à priori* a logical necessity. Nevertheless it appears to me to be desirable to trace the change of individuality, at least in the case of those "successive" fissions (*strobilation-form of fission* sensû latiori) which are of such frequent occurrence. In so doing I have no intention of entering at length into the theory of animal individuality; on the contrary, it is sufficient for our purpose to proceed from more general experience and considerations.

Starting from the fact that in many animals "the single individual can be split up by means of artificial division into several individuals which continue an uninterrupted existence," it was shown by Goette "that this divisibility is neither unlimited nor unconditional, but is without exception accompanied by the fact that the parts possess the structural conditions of the whole, and moreover the power of preserving them in integral continuity—that, in other words, they are capable of providing in themselves a complete repetition of the original whole; 'individuality' of organisms therefore does not signify absolutely an indivisibility, but rather only such as maintains the integrity of a vital unit or of a common life, and at the same time the possibility of an independent existence" †.

Goette therefore sees in individuality the "condition of

* G. v. Koch, "Die ungeschl. Vermehrung einiger paläozoischer Korallen vergleichend betrachtet," Paläontographica, Bd. 29, pp. 341 *et sqq.*

† A. Goette, 'Ueber den Ursprung des Todes,' Leipzig, 1883, pp. 12 *et sqq.*

certain relations of the parts to the whole;" this corresponds, however, to the stage which the organization has attained at the time, and is therefore "moreover dependent upon the origin and progress, in short the development of the organization."

This conception applies in the same degree to embryonic development as to reproduction of animals by fission or gemmation. In both cases the individuality of the animal which is coming into existence shows itself dependent upon the progress of the organic development, as a cohesion of definite relations of the parts to the whole, which becomes ever more and more consolidated concurrently with the organization. But naturally it is impossible that this cohesion should be a rigid one, the same for all animals—this is proved at once by the exceedingly variable degree to which the regenerative capacity is expressed; it will, on the contrary, be extensible within narrower or wider limits. Herein lies the *à priori* difference between fission and gemmation, as well as every other mode of reproduction, since the former necessarily postulates a loose arrangement of that cohesion, more readily dissoluble without injury to the common life; for were this not so the power of fission would be altogether suspended. The individuality of animals undergoing fission must therefore be of a fusible kind, so fusible that a continual change in the cohesion of the parts which form a whole is rendered possible, without occasioning disturbance to the common life.

Experience proves that in all cases of fission a portion of the original relations existing in the parent form is dissolved, and combines with those which now appear for the first time and which result from the development of new organs by regeneration to form a new unit; while the remnant of the old relations which is left behind either manifests by itself a unity which is viable or replaces the relations which have been lost by equivalent new formations. Thus, in *Microstoma* an animal divides in the first place into two individuals, whereby the original individuality is destroyed and superseded by the two new ones. The latter soon experience the like fate, and with the destruction of their individualities four fresh ones are constituted, and so on.

It is impossible to raise the objection that perhaps they are quite unimportant and trivial portions which are taken from the original animal and applied to the formation of one of the new individuals, and that therefore the individuality of the other zooid is essentially unchanged, since, indeed, it remains

in possession of the most important primary organs (central organ of the nervous system &c.); for the proportion of the original relations which are dissoluble is indeed limited by the conditions of the permanence of the common life, but within these limits is free, now greater, now smaller. Whether the posterior half or the posterior quarter or eighth of a *Microstoma* forms a new individual of itself is a matter of complete indifference for the character of the entire process. In other words, the division of a *Microstoma* into two equal halves is fundamentally the same process as its fission into two products, one of which consists of three quarters and the other of one quarter of the original animal, and so on.

A series of separate acts of fission, as exhibited by the species of *Microstoma* for instance, is in ordinary terminology usually referred to one animal as the mother-individual ("ancestress" ("Stammmutter") of von Graff); and if a number of units has been developed we are accustomed to say that the "ancestress" has given rise to so many daughter individuals. We are the more inclined to do this since separation sets in very late, so that the zooids remain for a time in connexion with one another and form temporary chains of individuals.

This view is, however, strictly speaking erroneous, for the ostensible "ancestress" is destroyed by the very first fission, and for the following one the two zooids which resulted from the first paratomy behave to their products as "ancestresses," precisely in the same way as their parent form did to them, and so on.

If therefore we say that the *Microstoma*-chains have arisen simply through fission we must be understood only to mean that these chains owe their origin to a series of paratomies, in which the final acts, the separations, appear postponed in regular sequence to relatively late periods. The reproduction of *Microstoma* therefore represents a combination of successive acts of fission, each separate one of which constitutes a paratomy.

From the standpoints which have been developed in the foregoing paragraphs, I would define fission and gemmation in the Metazoa as follows:—

*Fission is a process of separation of parts which originally belonged to an integral whole, and have arisen or are in process of origin by normal growth, wherein new individuals are formed by supplementary new formations, with destruction of the original unit.*

*Gemmation, on the contrary, is a process of new formation*

*of entire individuals, depending exclusively on a peculiar (differential) growth, which differs from the normal*; herein the budding vital unit is *usually* preserved unchanged.

## III.

I have no intention of here discussing separately the cases of reproduction by fission and gemmation which have been discovered up to the present time among the Metazoa. After what has been stated in the previous section there can scarcely be any necessity to do so, more especially since a series of instances of asexual reproduction, like that of the Tunicates, Bryozoa, and most of the Cœlenterates, is universally and without contradiction regarded as gemmation.

It is true that the case is different as regards the so-called *terminal gemmation* (*formation of buds at the end, strobilation* sensû latiori=*axial gemmation* of von Kennel *), under which are included the formation of *Ephyræ* in the Medusæ (originally strobilation *sensû stricto*), certain forms of reproduction in the Stony Corals, more closely characterized by Semper †, the formation of chains in the Microstomids (*Microstoma* and *Stenostoma*), and lastly the majority of modes of reproduction in the Annelids ‡.

Nevertheless even in these cases there is no further need for any detailed statements if I affirm that the above processes of asexual reproduction are instances of fission.

For as regards the strobilation of the Medusæ, in the first place, the two latest and most exhaustive investigators of the subject, Claus and Goette, have conclusively proved that herein, *even according to the customary method of representation*, fission, and not gemmation, takes place.

"For the proper comprehension of the phenomena of strobilation," writes Claus §, "it is before all things neces-

* J. v. Kennel, 'Ueber Theilung und Knospung der Thiere,' Dorpat, 1888, p. 17.

† C. Semper, "Ueber Generationswechsel bei Steinkorallen &c.," Zeitschr. f. wiss. Zool. Bd. 22, pp. 235 *et sqq.*

‡ The formation of proglottides in the Cestodes, which is included here by certain investigators as being likewise a case of "axial gemmation," may well be neglected, for the justification for considering the proglottides as a special generation of sexual animals, developing asexually from the Scolex, and therefore regarding the tapeworm as a dimorphic colony, as was persistently maintained by Leuckart ('Die Parasiten des Menschen,' Bd. 1, 2 Aufl., Leipzig, 1879–1886, p. 342), whose latest disciple is von Kennel (*op. cit.* p. 16), is still very doubtful.

§ C. Claus, 'Untersuchungen über die Organisation und Entwicklung der Medusen,' Leipzig, 1883, p. 16. Even to these statements of Claus I am able to attach but little weight, after what has been already men-

sary to bear in mind the fact that the regeneration of an Ephyra on the oral disk of the Scyphostoma, within the circlet of tentacles belonging thereto, has in no single case been proved. There is no terminal gemmation of Ephyræ on the oral disk of the Scyphostoma-polype; on the contrary, the rudiments of the disks of the Ephyræ are segments of the actual body of the Scyphostoma, which are marked off outside the circlet of tentacles by constriction of the wall of the cup, and are set free as sections of the body."

In opposition to Hæckel Claus insists * that "as a matter of fact the terminal portion of the Strobila which becomes the Ephyra—and for the sake of simplicity we will commence with the simplest and most typical form, that of the monodiscous Strobila—is no product of subsequent growth on the part of the Scyphostoma, but rather the anterior half of the body of the latter, which after previous uniform growth of the trunk of the Scyphostoma has marked itself off by constriction and proceeds to attain its liberty as a segment. Moreover, with the separation of the latter the primary individual, as such, is destroyed and split up into two new individuals, since the posterior individual also represents only a segment of the parent form. Both fission-products are coordinated to one another, for the basal stump, with or without a circlet of tentacles, nevertheless essentially corresponds to a Polype which is equivalent to a Medusa. Both Ephyra and Polype are consequently in their mutual relations comparable to an Infusorian in process of fission, of which only the one segment possesses a mouth and adoral zone of cilia, while the other is as yet without these structures or only exhibits them in course of formation. But should we wish to consider one segment as older than the other, and to subordinate the latter to the former, it would be more just to regard the hinder and less perfect segment as the younger portion, which would then be comparable to a terminal bud. In truth, however, from the point of view of ontogeny, they are both of the same age and equivalent to one another; yet the anterior segment differentiates sooner into a form which becomes free as a Medusa, while the posterior one subsequently undergoes regeneration and completion."

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tioned (*cf.* note *a*, p. 26); I quote them, however, in order to show that even those investigators who consider it superfluous to discuss whether we are dealing with fission or gemmation, nevertheless in a given case exert themselves diligently to answer the question.

* *Op. cit.* p. 17.

Goette * expresses himself in a precisely similar fashion :— "Since the first Ephyra-disk is only the further developed oral segment of the Scyphostoma, it naturally follows that it can in no way be regarded as a bud. That which reminds us of gemmation in it, *e. g.* the outgrowth of the circlet of lobes, belongs, just as does the previous outgrowth of the tentacles of the Scyphostoma—both of which processes are indeed termed 'sprouting' ('Hervorknospen') in looser phraseology—simply to the progressing development of the entire segment, which preserves its identity. It follows that the liberation of the first Ephyra can also be nothing else than the separation of two segments of an organism, both of which are in process of development, but were already in existence before—or, in other words, simple fission. On the abandoned peduncle of the monodiscous larvæ, however, the new Ephyra arises in precisely the same way as the first, by a transformation of what is originally its oral section into the disk of a Scyphostoma, which develops only secondarily into the disk of an Ephyra. For the formation of Ephyræ in the case of the monodiscous larvæ gemmation is therefore entirely out of the question. But owing to the agreement of this process in the case of the mono- and polydiscous larvæ this necessarily applies to the latter just as much as to the former. The disk of the Ephyra therefore never arises by gemmation, and thus strobilation is in all cases a simple fission of larvæ in process of development."

With regard to the phenomena which immediately succeed the actual separation of the Ephyra from the Scyphostoma, both in the case of the liberated Ephyra-Medusa as also in that of the Polype which is left behind, Goette † remarks that "therein is repeated merely a process of regeneration analogous to that in the development of any other organism with terminal mouth—be it a Worm, Infusorian, or anything else —whereby the general import of the previous or simultaneous process of fission is in no way prejudiced. It is likewise clear that in this respect the regeneration of the proboscis can be of no greater account than that at the gaping crown of the previously liberated Ephyra : both phenomena are inevitable accompaniments of fission, which the development of the first and all subsequent Ephyræ of a polydiscous Strobila cannot exhibit in materially different guise."

With reference to the supposed instances of gemmation

* A. Goette, 'Entwicklungsgeschichte der *Aurelia aurita* und *Cotylorhiza tuberculata*,' Leipzig, 1887, p. 50.

† *Op. cit.* p. 46.

which some years ago were stated by Semper to occur in certain Stony Corals *, it is to be remarked that some of them, in so far as the facts, which were principally derived from the skeletons, admit of such an interpretation at all, must be referred to processes conformable to the Strobila-formation of the Medusæ, *i. e.* must be regarded as cases of fission. This applies especially to *Flabellum variabile* and *Placotrochus lævis*. But as to Semper's statements about the asexual reproduction of his species of *Fungia* (which are not more closely specified), they have so little to do with adequate observations that a close investigation, particularly of the processes of growth as they occur in these forms, will have to be undertaken afresh before a satisfactory insight will be possible.

The numerous modes of reproduction in the Annelids, some of which are more thoroughly, but the greater portion only very superficially, known †, cannot be here discussed. Thus much, however, may be affirmed without immediate proof, that, so far as regards observations and not theories, gemmation has hitherto not been shown to exist with certainty in the segmented worms, with the exception of the peculiar budding form of *Syllis ramosa*. The pretended **lateral gemmation** of certain Annelids, which Pagenstecher ‡ believed he had observed, has already been rejected by Ehlers § as erroneous. It is true that the asexual reproduction of *Autolytus prolifer*, which was observed years ago by Frey and

* C. Semper, "Ueber Generationswechsel bei Steinkorallen &c.," Zeitschr. f. wiss. Zool. Bd. 22, pp. 235 *et sqq.*

† This applies especially to the reproduction of *Myrianida* (*Myriadina*) described by Milne-Edwards ("Recherches zoologiques faites pendant un voyage sur les côtes de la Sicile," Ann. Sc. Natur. (sér. 3), Zool. t. iii. pp. 170 *et sqq*). With regard to this M. Schultze says, "As a matter of fact, as is evident from his description, Milne-Edwards observed only a single specimen, which consisted of a series of seven individuals adhering to one another. From the series in question this investigator formulated his views as to the nature of the fission, which he supposed to be based upon a true formation of buds. But how difficult it is to decide from such scanty material, and without the closest microscopical investigation, whether a segment of the parent-form does or does not pass into the young, will be admitted by every one who has occupied himself with similar observations" (M. Schultze, "Ueber die Fortpflanzung durch Theilung bei *Nais proboscidea*," Arch. f. Naturgesch. 15 Jahrg., Bd. 1, p. 302). The numerous and scattered statements as to cases of asexual reproduction in Annelids altogether urgently need a critical sifting, in order to separate the observations from the speculations.

‡ A. Pagenstecher, "Untersuchungen über niedere Seethiere aus Cette," Zeitschr. f. wiss. Zool. Bd. 12, p. 267.

§ E. Ehlers, 'Die Borstenwürmer,' Leipzig, 1864–1868, pp. 211 *et sqq.*

Leuckart*, but has not since been investigated again, seems to a certain extent to present the appearance of gemmation; yet when considered in connexion with similar processes in the forms most closely allied (*Autolytus cornutus* and the true Syllidæ) it will certainly require another interpretation. Indeed it has been stated by Ehlers precisely with regard to the asexual reproduction of the Syllidæ (including *Autolytus*) "that there is here no question of fundamental differences, but that there merely takes place a development of the same process differing in degree" †. As a matter of fact we ought certainly not to perceive gemmation in the asexual reproduction of *Autolytus prolifer*, but merely an extreme one-sided development of the usual simpler mode of reproduction of the segmented worms.

It is evident from what has been stated that the asexual multiplication of *Microstoma*, which has the chief claim upon our attention in the present investigation, represents fission. That which was demonstrated by Claus and Goette for the formation of Ephyræ is perfectly applicable in all essential points to the fission of the Microstomids also, and it is sufficient to refer the reader to what has been quoted above from the writings of the investigators in question.

Since all forms of reproduction which have been regarded as instances of terminal gemmation thus prove to be cases of fission, we arrive at the result that a formation of terminal buds in the customary sense has no existence whatever.

## IV.

I have yet to allude to the statements of earlier investigators.

If we may neglect the more incidental assertions of older authors, E. Hæckel was the first who, although a long time ago, attempted systematically to establish the theory of fission and gemmation. In his classic 'Generelle Morphologie,' so rich in fresh points of view, this investigator wrote (1866): "In self-fission the growth of the individual which ushers in reproduction is total, and in the act of fission is destroyed in its totality, so that the products of fission are equivalent to one another. In the formation of buds, on the contrary, it is an isolated portion of the body of the individual which, by means of special growth, leads to the formation of a new indi-

* H. Frey and R. Leuckart, "Beiträge zur Kenntniss wirbelloser Thiere &c.,' Braunschweig, 1847, pp. 91 *et sqq.*

† E. Ehlers, *op. cit.* p. 208.

viduality (bud), and this then separates completely or incompletely from the parent individual without the latter's own individuality being thereby destroyed. Therefore in this case the two products of fission are of unequal value." Hæckel further proceeds to show that fission produces individuals of the same age, whereby the original animal as such is abolished, while the products of gemmation are of different ages, and the budding animal continues to exist unaltered as the parent form *.

These assertions, the artificial construction of which is unmistakable, met with just contradiction on the extension of our knowledge of the processes in question. Thus Goette took the special case of the strobilation of *Aurelia aurita* as the starting-point of a critical excursus, in which he in the first place alludes to the fact that the products of gemmation resemble the parent form far more often than do those of fission. He then goes on to say: "What Hæckel moreover means by the unequal age of the products of gemmation is shown by the application to the case of Strobila which follows upon the heels of the definition; for he says that the disks of the Strobila arise one after the other, and so possess that inequality of age which is the characteristic of gemmation. He therefore refers in this case not to the difference in age between the products of division due to one individual process of gemmation, but rather to the different age of the disks which follow one another in succession. Precisely the same difference of age exists, however, in all successive fissions of the same animal, such as, for instance, appear so conspicuously in *Microstoma*; it is therefore quite useless as a distinctive characteristic of gemmation.

"Just as untrustworthy is, lastly, the characteristic of growth, in the one case total (fission), in the other only partial (gemmation); for, apart from the frequent difficulty of such a distinction, we are in no wise justified by experience in declaring a growth at all to be the necessary cause of every division."

Goette, therefore, is unable to recognize as applicable and sufficient the distinguishing characters of fission and gemmation laid down by Hæckel, and for his part defines fission as a "separation of connected parts, which were therefore already present in a fully developed state," but gemmation as a "new formation of parts by the method of a local growth, which become more or less independent" †.

* E. Hæckel, 'Generelle Morphologie der Organismen,' Bd. 2, Berlin, 1866, pp. 37 *et sqq.*

† A. Goette, *op. cit.* pp. 47 *et sqq.*

Very recently the customary views upon fission and gemmation, which conform more or less to Hæckel's statements, have also been criticized and rejected by von Kennel, who in so doing arrives at the conclusion "that neither equality or inequality of the products of division, nor difference or agreement of age, nor even the possibility of distinguishing between the original and the new individual, furnish us with the means of separating fission and gemmation" *.

It appears to me to be superfluous to add anything further to the critical statements of Goette and von Kennel, with the results of which I am in accord. As regards Goette's definitions of fission and gemmation which are quoted above, they confine themselves too strictly to conditions which are of importance for the special question of the interpretation of strobilation to suffice for a more general application. I therefore turn to the definitions of the conception of fission and gemmation which have lately been developed in comprehensive fashion by von Kennel.

"If we compare all reproductive processes with one another," says von Kennel, "we find that in one group the mass of the products proceeding from the reproduction, when taken together, is equal to the mass of the original individual before the commencement of the visible changes by which the process was ushered in. In all other cases reproduction is introduced by the appearance of new portions, which have nothing to do with the individual, through an accession of organized substance, so that the sections, after becoming independent, represent in their entirety more mass than was possessed by the original animal before the appearance of the reproductive phenomena. We may term the former class fission, the latter gemmation" †.

It follows from this that von Kennel regards the presence or absence of growth as the sole criterion of gemmation or fission respectively. That in the case of the latter at any rate von Kennel's definition betokens an artificial and arbitrary limitation is manifest without further comment.

But if we follow out von Kennel's assertions to their logical conclusion we arrive at the result that no instances whatever of fission occur within the limits of the Metazoa. **For it is impossible to mention any case of asexual reproduction in these animals in which "the mass of the products proceeding from the reproduction when taken together is equal**

* J. v. Kennel, 'Ueber Theilung und Knospung der Thiere,' Dorpat, 1888, p. 14.

† J. v. Kennel, *op. cit.* pp. 14 *et sqq.*

to the mass of the original individual before the commencement of the visible changes by which the process was ushered in;" because every instance of fission in the Metazoa is, and must be, inevitably combined with regenerations or new formations of another kind. But these just as necessarily entail an increase in organic substance.

Now it is certainly no reason for claiming a process as an instance of fission to say that if we did not fission would entirely disappear as a method of reproduction in the Metazoa. But von Kennel himself designates as fission the asexual reproduction of *Planaria subtentaculata*, which has been described, it is true only imperfectly, by Zacharias *, and has moreover acquainted us with the interesting multiplication of a freshwater Triclad, which he terms "transverse fission," although in both cases, having regard to the regenerative processes which ensue, an increase in organic substance is undeniable †.

Fundamentally von Kennel's conception of fission is exhausted with the bare process of separation, therefore with that which I have termed "dissection" within a case of paratomy. It is therefore postulated by this investigator that, when we would speak of fission in animals, the process in question must be identical with the splitting of a block of stone. This, however, according to animal organization is impossible.

Von Kennel's conception of gemmation is in no better case. If, as we have seen, practically nothing remained for fission, gemmation, according to von Kennel, includes all instances of asexual reproduction in which any sort of growth appears. It is consequently a matter of complete indifference whether the particular process of growth takes place in the animal as a speciality, leaving the individual manifestation thereof unaffected, or whether it coincides with the normal increase in size of the creature, as we also meet with it in the animal's nearest allies, which, however, lack the faculty of asexual reproduction.

The gemmation of a Salp or Bryozoon, the formation of Ephyræ in the Medusæ, the processes of strobilation in the Worms, the gemmation of Hydroids and Corals, &c., are accordingly the same in principle, so much so indeed that, as v. Kennel ‡ in the first instance, and, independently of him,

* O. Zacharias, "Ergebnisse einer zoolog. Excursion in das Glatzer-, Iser-, und Riesengebirge," Zeitschr. f. wiss. Zool. Bd. 43, pp. 271 *et sqq.*

† J. Kennel, "Untersuchungen an neuen Turbellarien," Zool. Jahrb. Bd. 3, Abth. f. Anat. u. Ont. der Thiere, pp. 407 *et sqq.*

‡ J. v. Kennel, 'Ueber Theilung und Knospung der Thiere,' pp. 17 *et sqq.*

Lang *, almost simultaneously endeavoured to render probable, all these processes are referable to one and the same starting-point—the regenerative faculty of animals †.

Nothing appears to me to be so characteristic of von Kennel's view of gemmation as the following statements by him ‡:—"There appear . . . . in many Annelids, such as *Nais*, *Chætogaster*, *Æolosoma*, *Syllis*, &c., new structures nearly in the middle of the segmented body, owing to which the anterior and posterior halves of the body are pushed away from one another. If this newly intercalated region of the body differentiates into a larger number of young segments, which further develop partly into new cephalic somites for the section of the body which lies behind them, and partly into new trunk-segments for that which lies in front—it is manifest that a formation of buds is thereby constituted, for in the original individual a new formation has appeared which is at first small, but is nourished by the original form and increases in size. If this bud subsequently constricts more and more about at its middle until complete separation takes place, we can scarcely be contradicted if we term it a case of reproduction by gemmation."

Here, therefore, v. Kennel designates as a bud the "new formation, which is at first small, but is nourished by the original form, and increases in size." This supposed bud, which in truth represents nothing else than the so-called zone of gemmation (zone of regeneration), is no individual at all, no organic person, but **a mixtum compositum, formed from the posterior and anterior halves of two different animals, attached together by their opposite ends**; and for the origin of these two there finally remains no other method after all, except—fission.

Moreover it is at once evident that v. Kennel is here considering cases of fission which, as we are wont to express it, depend upon processes of gemmation, and, designating the special kind of definite regenerative processes as processes of

* A. Lang, 'Ueber den Einfluss der festsitzenden Lebensweise auf die Thiere &c.,' Jena, 1888, pp. 108 *et sqq.*

† From my standpoint I am naturally unable to assent to this view, especially in this generalization. **The faculty of reproduction by gemmation and fission and the power of regeneration may certainly depend upon the same general primary causes**; but with this nothing is stated as to the special causes, in consequence of which fission has been developed in one case and gemmation in another. The cutting off of a tentacle is, it is true, the external stimulus for its regeneration, but it is not the cause of the power to replace the lost part.

‡ *Op. cit.* p. 13.

gemmation, interprets the whole mode of reproduction simply as gemmation.

When v. Kennel further divides the manifold forms of gemmation into *axial* (strobilation *sensû latiori*) and *lateral**, this distribution is also of little value, since it is based *solely* upon the difference in the direction of the growth, and therefore a similarity of the processes in question in other respects is tacitly affirmed, which is by no means the case. Besides it is in many instances a matter of purely personal interpretation whether the actual bud is regarded as lateral or terminal (origin of many Hydromedusæ by gemmation).

In other words, **whether an animal, as such, grows, and during the growth or subsequently divides itself into a number of individuals, or whether an animal by a special growth upon itself produces new zooids, are two entirely different processes; at any rate their difference is far greater than that between the questions whether the buds arrive at their development upon an animal at the side, in front, or behind, provided only that their formation agrees in other respects.**

I am therefore not in a position to recognize as really well-grounded the distinguishing characteristics of fission and gemmation which are laid down by v. Kennel, apart from the fact that they also convey no advantage for the praxis of a simpler discrimination between the two modes of reproduction.

## V.

On referring to the foregoing statements it may be asserted that fission and gemmation can well be distinguished from one another. While all forms of reproduction which were referable to the natural conception of fission were brought into one division, a general characteristic was disclosed for those methods also which remained outside that series, in the special character of the growth which appears in connexion with them. This separation of two widely distributed forms of asexual reproduction is, however, not to be maintained merely from the practical point of view of facility of systematic survey; but it is also not devoid of a deeper meaning: **the intimate relation between fission and gemmation is, at least to the extent to which it is nowadays so frequently accepted, a fiction.**

Without of course wishing to deny all connexion between

* *Op. cit.* p. 17.

fission and gemmation *, that conception nevertheless could well have its foundation only in the supposition that not merely do fission and gemmation merge into one another through unequivocal intermediate forms, but that also there is justification for venturing to speak of both modes of reproduction in the general sense; for only on such hypotheses would it be permissible to extend to all cases definite results of the facts found in one or more, and to elevate them into a principle of general applicability.

The conditions alluded to, however, by no means occur.

As regards possible **transitional forms**, in the first place it certainly appears to be beyond doubt that, especially among the Cnidaria, the existence of such intermediate modes of reproduction cannot be gainsaid. Yet these supposed intermediate forms assume this aspect solely in consequence of the faulty and indefinite character of the views which have hitherto been held. **Intermediate forms of this kind occur in the Cnidaria just as little as in the Worms or any other Metazoa.** Von Koch was entirely in the right when, on the basis of his minute investigation of the conditions of asexual reproduction, which were, it is true, chiefly those of the Palæozoic Corals, he was induced to create a "fission-gemmation" ("Theilungsknospung"), and included it, as well as his "septal gemmation," under fission, according to customary views †. Yet, according to the aspects which influence me, it is no less clear that, in the forms of gemmation alluded to, I am bound to recognize real gemmation and not fission.

The instances of asexual reproduction in the Worms, in spite of all differences of detail, nevertheless exhibit so uniform a general character as to necessitate similar interpretation. In contrast to these conditions the remarkable gemmation of *Syllis ramosa* ‡ appears completely isolated; as yet this represents the sole case of gemmation in the Annelids, and is probably a purely personal acquisition on the part of this Syllid, which has been gained in adaptation to the fundamentally altered mode of life.

* By this I allude not merely to the connexion which is entailed by the community of the same primary causes (*cf.* last note), but also to that which would, as it were, be implied by the proof that a particular case of fission could, in its origin, be traced to a particular case of gemmation, or *vice versâ* (*e. g.* origin of strobilation, according to Claus—'Untersuchungen über die Organisation und Entwicklung der Medusen,' Leipzig, 1883, p. 18).

† G. v. Koch, "Die ungeschl. Vermehrung einiger paläozoischer Korallen vergleichend betrachtet," Paläontographica, Bd. 29, p. 89.

‡ "Report of the Scientific Results of the Voyage of H.M.S. 'Challenger,' Zoology," vol. xii. pp. 198 *et sqq.*

The second point, whether fission and gemmation may be conceived in a general sense, is in no better case. No one will wish to maintain that the various kinds of fission as well as the manifold cases of gemmation have been inherited through the animal series from their first appearance, and should consequently be regarded as phyletic units. But also as regards their origin fission and gemmation cannot have proceeded from the same causative conditions.

From the facts which we have before us an origin of the same kind cannot be exhibited for the series of those modes of reproduction which are to be designated as cases of gemmation; on the contrary, it is in the highest degree probable that the gemmation of the Salps and that of the Bryozoa represent specific acquisitions within the respective phyla. Although at the present time no certain decision is possible as to the way in which these acquisitions were developed, nevertheless the wide-reaching investigations of Seeliger have sufficiently demonstrated that the formative laws of gemmation in the Bryozoa are of an entirely different character from those which have had effect among the Tunicata *.

With reference to the quite aberrant gemmation of *Syllis ramosa*, I have already remarked above that the active causes of its origin may well be sought without hesitation in the specialities of its peculiar mode of life.

The cases of gemmation among the Cnidaria are in no way lacking, as it appears, in a more homogeneous character, which may well indicate a common originating cause.

Although it follows that the conditions under which the manifold instances of gemmation may have arisen in the various animal phyla are at present in a great measure still an object of pure conjecture, nevertheless that which is actually known about them in the several cases or series presents results of so heterogeneous a nature that the justification for generalizing about gemmation is at least not proved.

The same applies to fission.

The strobilation-forms of this process in the Cnidaria and Worms, which are usually selected for comparison, have in truth a mere external similarity only. Owing to the great agreement which is exhibited in essential features by all cases of fission in the Worms, we shall have to consider them as a development pointing to a common basis; for this development the conditions of the origin of those modes of repro-

* O. Seeliger, "Die ungeschlechtliche Vermehrung der endoprocten Bryozoën," Zeitschr. f. wiss. Zool. Bd. 49, p. 204.

duction were supplied within the phylum of these animals themselves and their peculiar circumstances. In the same way, too, this point of view may well be adopted for the Medusan Strobila also, no matter whether we would derive it with Claus * from the gemmation of stolons or not.

We thus arrive at the final result, that the customary idea of the intimate relationship between fission and gemmation has no justification in facts, but rather that the separation of the asexual reproductions of the Metazoa possesses not only a notional meaning, but also a real foundation.

**The cases of asexual reproduction in the various animal phyla have proceeded independently of one another from conditions existing within these phyla,** so that that which, it may be, can be rendered probable for a single case of reproduction or for a congeries of similar cases, includes no binding force for other instances of multiplication by fission or gemmation.

It will be the task of future investigation, in determining the originating causes which have decided the character of each form of reproduction belonging to the present category, to separate chaff from wheat, so to speak, *i. e.* to eliminate from the series of **propagations** those modes of multiplication which represent mere **augmentations.** Merit is due to von Kennel for having emphatically drawn attention to this important difference †.

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## VII.—*On some undescribed* Cicadidæ, *with Synonymical Notes.* By W. L. Distant.

It has been urged, and with some reason, that descriptive papers should, where possible, be confined to the diagnoses of members of some particular zoological region; and if this course could always be pursued the convenience it would afford to purely faunistic workers would doubtless be great. But the formulation of rules and theories is often a very special gift of a very few, and is sometimes in an inverse ratio to possibilities and experience. There is, however, a course which will enable the descriptions of widely distributed insects to be faunistically apprehended, and that is by geographically tabulating the species described in some manner similar to the following, which applies to the present paper.

* C. Claus, 'Untersuchungen über die Organisation und Entwicklung der Medusen,' Leipzig, 1883, p. 18.

† J. v. Kennel, 'Ueber Theilung und Knospung der Thiere,' p. 8.